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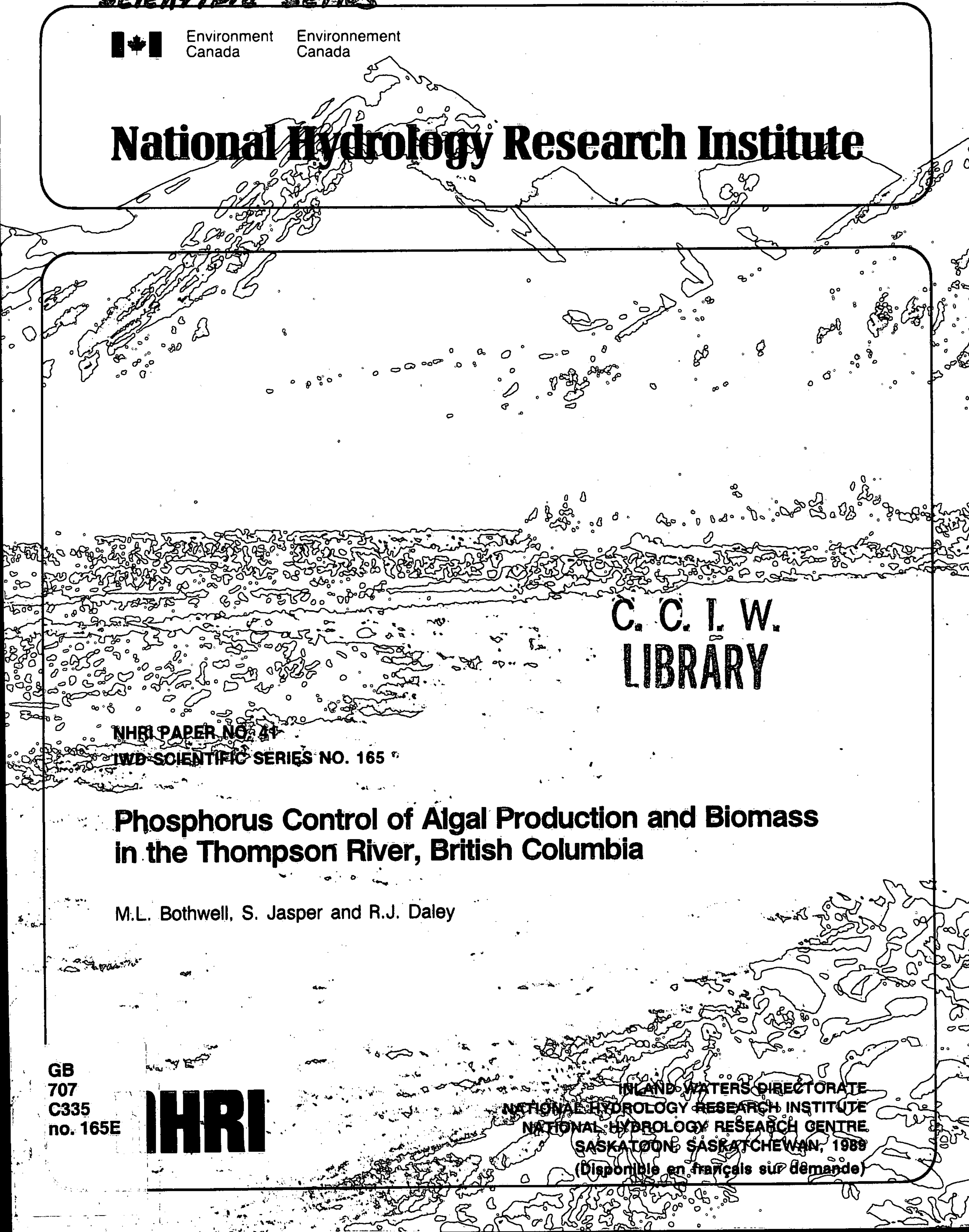

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M.L. Bothwell, S. Jasper and R.J. Daley

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# Contents

# Illustrations

# Illustrations (Cont.)

# Abstract

The first phase of the experimental trough research program undertaken jointly by the Inland Waters Directorate of Environment Canada and Weyerhaeuser Canada Ltd. during 1980–81 established that the higher algal biomass levels in the Thompson River downstream from Kamloops Lake were caused by phosphorus originating from point source discharges near Kamloops. These early experimental comparisons of algal growth rates in the North, South and lower Thompson rivers indicated that at soluble reactive phosphorus concentrations of 3–4 ppb, periphytic algae in the lower Thompson River were growing at or near the maximum rate possible during the critical late winter—early spring period.

The second phase of the program consisted of extensive controlled phosphorus addition experiments conducted at Chase, B.C., during 1984–86. These experiments have conclusively established that the growth rates of periphytic diatoms in the Thompson River saturate at very low phosphate concentrations (at less than 1 ppb). Long-term algal biomass accumulation experiments, also conducted at the Chase experimental site, have shown that the maximum biomass of algae attained in flowing water also shows saturation kinetics. However, the concentration of phosphate required to saturate the sustainable standing crop of periphytic diatoms is considerably higher (about 30 ppb) than that which saturates cellular growth rate. In spite of continued algal biomass response with higher levels of P-addition, the shape of the biomass saturation curve means that a one-for-one, removal of phosphorus vs. reduction of algae is not expected.

Assuming that the average concentration of readily available phosphorus in the lower Thompson River is elevated by the pulpmill effluent by about 2.5 ppb during the low flow period, it is possible to predict roughly the downstream response in algal biomass that might result from a given percentage reduction in P-loading. Using data on the maximum sustainable algal biomass in response to phosphate additions, a simple analysis indicates that a 50% reduction in phosphorus from the mill effluent would result in less than a 20% improvement downstream. To achieve a "significant" improvement downstream, i.e., a 60% reduction in algal biomass, at least 90% of the available soluble phosphorus in the effluent would have to be removed. This finding suggests that additional efforts to control downstream algae by removing phosphorus from the pulpmill effluent would be relatively ineffective. Furthermore, recent observations that the "nuisance" levels of algae reported in the 1970's are no longer present suggest that additional nutrient control measures in the future may not even be necessary.

# Résumé

La première phase du programme de recherche en canal expérimental, réalisée conjointement par la Direction générale des eaux intérieures d'Environnement Canada et Weyerhaeuser Canada Ltd. en 1980–1981, a permis d'établir que les niveaux élevés de la biomasse algale dans la rivière Thompson en aval du lac Kamloops étaient attribuables à la présence de phosphore provenant de sources locales de déversement près de Kamloops. Ces premières comparaisons expérimentales des taux de croissance des algues dans les rivières Thompson nord et sud, ainsi que dans la partie inférieure de la rivière, ont indiqué qu'à des concentrations de phosphore réactif soluble de 3–4 ppb, les algues périphytoniques dans la partie inférieure de la rivière croissaient pratiquement au taux maximal possible pendant la période critique de la fin de l'hiver et du début du printemps.

Dans la seconde phase du programme, menée à Chase (C.-B.) au cours de la période 1984–1986, on a effectué des expériences détaillées sur des additions contrôlées de phosphore. Ces expériences ont clairement démontré que les taux de croissance des diatomées périphytoniques dans la rivière Thompson atteignent le point de saturation à des concentrations très faibles de phosphate (moins de 1 ppb). Des expériences sur l'accumulation de la biomasse algale à long terme, aussi réalisées au site expérimental de Chase, ont montré que la biomasse algale maximale atteinte dans des eaux en écoulement présente également une cinétique de saturation. Toutefois, la concentration de phosphate requise pour mener au point de saturation la culture sur pied durable de diatomées périphytoniques est de beaucoup supérieure (environ 30 ppb) à celle qui sature le taux de croissance cellulaire. Malgré la réponse continue de la biomasse algale à l'augmentation des niveaux d'addition de phosphore, la forme de la courbe de saturation de la biomasse montre qu'on ne peut s'attendre à ce qu'il existe une relation biunivoque entre l'extraction du phosphore et la réduction de la quantité d'algues.

En supposant que la concentration moyenne de phosphore directement disponible dans la partie inférieure de la rivière Thompson est accrue par l'effluent de l'usine de pâte à papier d'environ 2.5 ppb pendant la période de faible débit, on peut prévoir approximativement la réponse, en aval, de la biomasse algale qui pourrait résulter d'un pourcentage donné de réduction de la charge en phosphore. Une simple analyse des données sur la biomasse algale maximale pouvant être maintenue en réponse à des additions de phosphate révèle qu'une réduction de 50 % du phosphore provenant de l'effluent de l'usine procurerait une amélioration de moins de 20 % en aval. Pour obtenir une amélioration <<significative>> en aval, c'est-à-dire une réduction de 60 % de la biomasse algale, il faudrait extraire au moins 90 % du phosphore soluble disponible dans l'effluent. Ce résultat montre qu'il ne serait pas rentable de déployer des efforts additionnels pour extraire le phosphore de l'effluent de l'usine, dans l'intention de lutter contre la formation d'algues en aval. En outre, selon des observations faites récemment, le degré de <<nuisance>> des algues qu'on signalait dans les années 1970 n'est plus le même aujourd'hui, de sorte qu'il ne serait peut-être même pas nécessaire de prendre d'autres mesures de contrôle des éléments nutritifs dans l'avenir.

# Acknowledgments

This project was jointly funded by Environment Canada and Weyerhaeuser Canada Ltd. Technical support was provided by M. Bolin, R. Mitchell and K. Suzuki. The site for these experiments was kindly provided by the Village of Chase, British Columbia. The administrative support and encouragement of L. Adamache are gratefully acknowledged.

# Phosphorus Control of Algal Production and Biomass in the Thompson River, British Columbia

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## HISTORICAL BACKGROUND

Following commencement of operations at the Weyerhaeuser Canada Ltd. pulpmill in Kamloops in the late 1960's, numerous complaints from both the general public and fisheries biologists about water quality degradation problems in the Thompson River below Kamloops Lake were voiced. The three primary areas of concern were (1) taste and odour problems in the fish flesh, (2) colouring and foaming in the river, and (3) massive accumulations of algal slime on the rocks. A federal-provincial Task Force established in 1973 to address these questions concluded that the first two concerns either were not well supported by sound scientific facts or were primarily of an aesthetic nature, i.e., they did not appear to be of major ecological importance. The algal growth problem, however, was well documented scientifically and was potentially a risk for both fishermen (slippery rocks) and fish (intragravel oxygen depletion). The Task Force's final report in 1976 identified phosphorus loadings from both the Weyerhaeuser pulpmill and the City of Kamloops municipal sewage discharges as responsible for the high levels of algae in the lower Thompson River. Therefore, in 1976, the City of Kamloops began practising winter holdback and tertiary treatment of their effluent. These actions effectively reduced by at least one-half the point source phosphorus loadings to the Thompson River. Although the algal blooms below Kamloops Lake diminished somewhat in the late 1970's and early 1980's, the problem still persisted.

The Task Force presented strong and compelling evidence that phosphorus was the cause of the algal infestations. However, the arguments were indirect and circumstantial. In 1976, there was no evidence available to prove directly whether the periphytic algae in the Thompson River downstream from the P-inputs were physiologically more phosphorus-rich or were in fact actually growing faster than algae at upstream locations. These two central questions required answers before a reasonably conclusive judgement could be made that the algal slime accumulations in the lower Thompson River in the early 1970's were the result of point source P-loadings from the Kamloops area.

In 1979, experiments were proposed to answer these two key questions. An agreement for a jointly funded research project between Environment Canada's National Water Research Institute and Weyerhaeuser Canada Ltd. was reached in the fall of 1979. The research conducted during the winters of 1980 and 1981 involved the use of experimental troughs located on the banks of the North, South and lower Thompson rivers. These troughs simultaneously compared algal growth rates and phosphorus physiology in the three rivers under controlled physical conditions (Bothwell and Daley, 1981; Bothwell, 1983; Bothwell and Jasper, 1983; Bothwell, 1985). The results of these experiments confirmed the conclusion of the 1976 Task Force report, i.e., that phosphorus was in fact responsible for the excessive algal accumulations in the Thompson River. They showed for the first time that (1) soluble phosphorus concentrations downstream from Kamloops Lake were consistently higher than in the two upstream tributaries and (2) the periphyton algae downstream were physiologically responding to the higher phosphorus levels and were growing faster.

In spite of the strong connection established between P-loading and the algal problem downstream, it was still not possible in the early 1980's to predict the amount of improvement (reduction in algal biomass) to expect from a given reduction in the loading. (The one obvious exception to this would be if anthropogenic P-loading were to be eliminated entirely. In this case, the improvement would be 100%, i.e., all other factors being equal downstream, amounts of algae should be no different than before the advent of the cultural enrichment.) One reason for the difficulty in predicting downstream response to partial P-removal is that the relationship between algal growth and phosphorus concentration in flowing waters is a rectangular hyperbola. Similar saturation curves characterize most types of biological responses. A cost-benefit analysis for removal of phosphorus from the Weyerhaeuser Canada pulpmill first required that the shape of these curves be established. To this end another agreement for cooperative research was negotiated between Environment Canada and Weyerhaeuser Canada Ltd. in 1983. This new contract funded sophisticated phosphorus addition experiments conducted between 1984 and 1986 at the experimental troughs research apparatus (EXTRA) near Chase, British Columbia (Fig. 1).

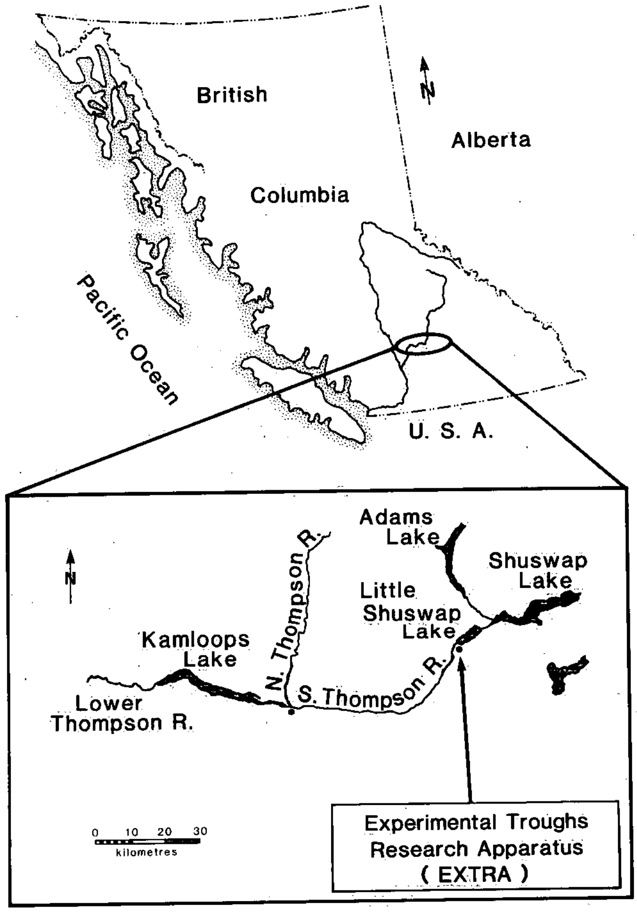

Figure 1. **Map showing the location of the experimental troughs research apparatus (EXTRA) near the outlet of Little Shuswap Lake in south-central British Columbia.**

This report summarizes the main findings of this final phase of the research project on phosphorus control of algal production and biomass in the Thompson River. Only those experiments and data germane to assessing the efficacy of tertiary treatment (P-removal) of the Weyerhaeuser Canada effluent, as a means of ameliorating the Thompson River algal "problem" downstream from Kamloops Lake, will be presented. A glossary of the technical terms frequently used in this report is provided at the back.

## RESULTS AND DISCUSSION

### Periphytic Diatom Growth Rates

One of the primary conclusions from the intersite comparison experiments conducted in 1980–81 was that growth rates of periphytic diatoms saturate at low phosphate concentrations (Bothwell, 1985). This conclusion was drawn on the basis of a limited number of observations and without precise knowledge of what the actual concentration of orthophosphate was in the rivers. Nevertheless, based largely on physiological evidence [alkaline phosphatase activity (APA), cellular N:P and C:P ratios], algae in the lower Thompson River appeared to be growing at or near maximal rates even though soluble reactive phosphorus levels were only 3–4 ppb.

This conclusion from the earlier research has now been confirmed and proven to be correct beyond any reasonable doubt. In fact, the levels of phosphate that saturate specific growth rate are much lower than previously expected. In ten separate experiments during 1984–1985 using enrichment levels of 0.1, 0.2, 0.5, 1.0, 2.0 and 5.0 ppb of orthophosphate-P, the specific growth rates ($\mu$ = divisions per day) of the algal communities always saturated at less than 1.0 ppb (Bothwell, 1988). The rectangular hyperbolic nature of the growth rate vs. phosphorus concentration curves at different times of year is clearly apparent (Fig. 2). While all curves saturate at low phosphorus concentrations, the maximum growth rate ($\mu_{max}$) at different times of year varied. The seasonal differences in the maximum rate are largely determined by temperature, i.e., at higher temperatures, growth rates with elevated levels of phosphorus are higher (Fig. 2).

If the specific growth rates are normalized to $\mu_{max}$ in each experiment and plotted against phosphate concentration, all the curves appear to be the same throughout the year (Fig. 3). The fact that the relative specific growth ($\mu$:$\mu_{max}$) response of algae to P-enrichment is similar year-round reaffirms that normalizing $\mu$ to $\mu_{max}$ factors out the major effects of physical factors controlling growth rate.

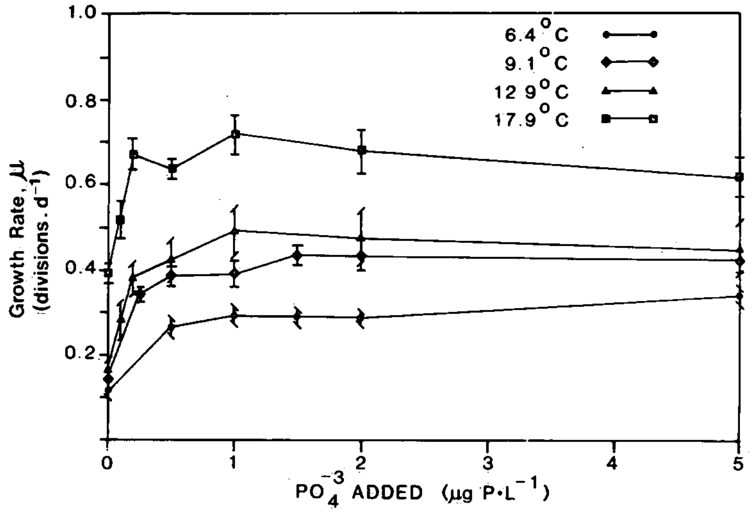

**Figure 2.** Growth rate (μ) of South Thompson River diatoms in divisions per day vs. added phosphate concentration at different temperatures (i.e., different times of year).

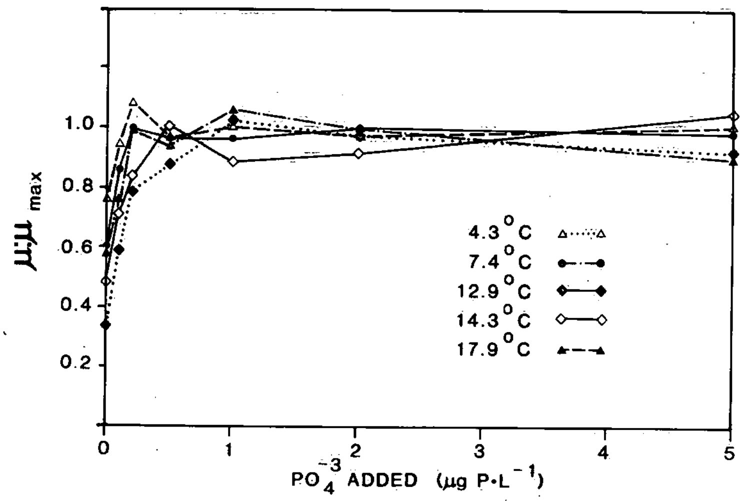

**Figure 3.** Relative specific growth rate ($\mu:\mu_{max}$) of South Thompson River diatoms vs. added phosphate concentration at different temperatures (i.e., different times of year).

## Phosphorus Control of Algal Biomass

Most of the experiments have focused on the effect of phosphorus on algal growth rates. The reason for this was the belief that the only way for a nutrient like phosphorus to affect changes in the biomass of algae in a river was to do so by altering their growth rates. Still, the primary motivation for this study was to find out how phosphorus influenced algal biomass. To test this directly, three long-term studies were conducted to determine how areal algal biomass in flowing troughs would be influenced by phosphorus concentration and to see whether this relationship differed substantially from the phosphorus-growth rate relationships.

Figure 4 shows the time-course changes in algal biomass during one of the long-term (59 days) experiments (Oct.–Dec. 1984). In these trials, biomass increased exponentially for a period of about two weeks, reached a plateau, and then, if the experiment was long enough, began to decline. The relationship between P-concentration and areal biomass was assessed in two different ways. First, nutrient levels were related to sustainable biomass (SB). For each P-addition of every experiment, SB was estimated by averaging the higher Chl *a* values

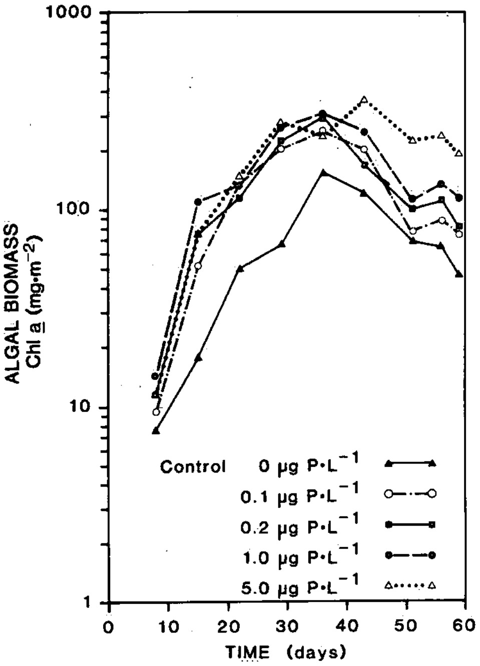

**Figure 4.** **Time-course curves of the periphyton biomass at different phosphate additions during a long-term experiment (Oct.-Dec. 1984).**

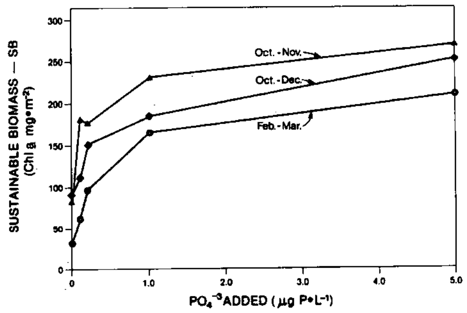

**Figure 5.** **Sustainable algal biomass (SB) in response to phosphate addition during the three long-term experiments.**

toward the end of each experiment. The highest SB value observed in each experiment was termed the maximum sustainable biomass, $SB_{max}$, which was used to normalize the other values.

For the second approach, nutrient levels were related to only the peak biomass (PB) observed in each treatment. The highest PB in each experiment was termed the maximum peak biomass, $PB_{max}$. The responses of $SB:SB_{max}$ and $PB:PB_{max}$ to P-enrichment were similar. For this reason and the sake of simplicity, only the SB data will be presented in this report.

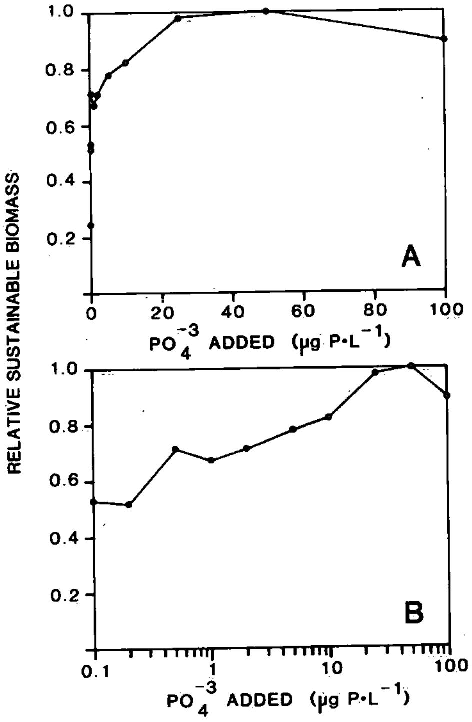

**Figure 6.** **Relative sustainable algal biomass ($SB:SB_{max}$) in response to phosphate additions up to 100 ppb during a long-term experiment (Oct.-Nov. 1985).** ***A*** **— Phosphate additions are plotted on a linear scale.** ***B*** **— The same data is in** ***A*****, but the phosphate values are plotted on a log-scale.**

The validity of the SB vs. P-concentration experiments is strengthened by the fact that the SB curves show saturation at higher P-levels (Fig. 5). As with the plots of specific growth rate, different curves were obtained at different times of year. The SB curves, however, differ from the specific growth rate curves in one very important respect: they do not saturate at low phosphorus levels. Biomass continues to increase up to 5 ppb and beyond. In one experiment (Oct.-Nov. 1985), where concentrations of phosphate-P all the way to 100 ppb were used, biomass continued to respond up to 25–50 ppb (Fig. 6A). When these same data are plotted on a semi-log scale (Fig 6B), a log-linear relationship between phosphorus concentration and SB is apparent, with saturation occurring near 30 ppb.

There is a simple explanation for the disparity between saturating P-concentrations for $\mu:\mu_{max}$ and $SB:SB_{max}$. While growth rates of individual cells and thin periphyton films saturate at low phosphorus concentrations, growth of the community as a whole does not. As algal accumulations become more dense, cells within the mat may become P-limited, while those closer to the surface of the periphyton matrix remain P-replete. Hence, higher concentrations of phosphorus in the overlying water should augment growth rates of cells deeper in the matrix by increasing the supply rate of the limiting nutrient.

### Seasonality of Phosphorus Limitation

The response of $\mu:\mu_{max}$ to P-additions shown in Figure 3 appears to be the same year-round, suggesting that the background concentrations of dissolved phosphorus in the South Thompson River do not vary seasonally. This is at odds with measurements taken in 1980–81 of soluble reactive phosphorus (SRP) and total dissolved phosphorus (TDP) in the Thompson River system as well as periphyton APA data, all of which indicated lower amounts of available phosphorus during the spring than in the winter (Bothwell and Daley, 1981; Bothwell, 1985). Although SRP concentrations in the South Thompson at Chase during 1984–85 showed no seasonal change (Bothwell, 1988), the APA data did show distinct temporal trends consistent with the earlier observations, indicating much higher phosphorus deficiency during the late winter through summer than during the fall and early winter (Fig. 7).

A paradox is perceived when a comparison is made between Figure 3, which suggests that the background level of available phosphorus in the South Thompson River is constant throughout the year, and Figure 7, in which the APA data indicate exactly the opposite. This is the result of the scale on which the data in Figure 3 are plotted. The relative growth rate responses to the addition of very low levels of phosphate in fact differ throughout the year. This is clearly shown in Figure 8. Here the $\mu:\mu_{max}$ values for 1984–85 are shown for only the control and the lowest levels of P-addition. The relative specific growth rate of algae in the control trough (with no phosphorus added) varies seasonally. Maximum values, indicating low phosphorus deficiency, occur during fall and midwinter, while low values (high phosphorus deficiency) are present in early spring through summer. When the algae are not very P-limited, the addition of very small amounts of phosphate (less than 0.1 ppb) results in growth rate saturation. Under more phosphorus limited conditions, additions of 0.5 ppb phosphate are needed to saturate growth rates (Fig. 8). This means that background levels of readily available phosphorus in the South Thompson River vary seasonally (Bothwell, 1988). Data from the earlier 1980–81 intersite comparison (Bothwell and Daley, 1981; Bothwell, 1985) suggested similar seasonal changes occur in the North Thompson River as well. This information is important in determining those times of the year when river algae will respond the most to P-loading.

APA data from the control algae can be used as an indicator of the degree of phosphorus deficiency in the river. Taking values of less than 100 nmoles·$\mu g^{-1}$ Chl $a \cdot h^{-1}$ as being indicative of low P-deficiency, the period from approximately October through January would show less response to P-loading than at times of the year when APA exceeds 100, i.e., from roughly February through August (Fig. 8). The exact timing of these periods may vary from year to year, but the general pattern probably remains the same.

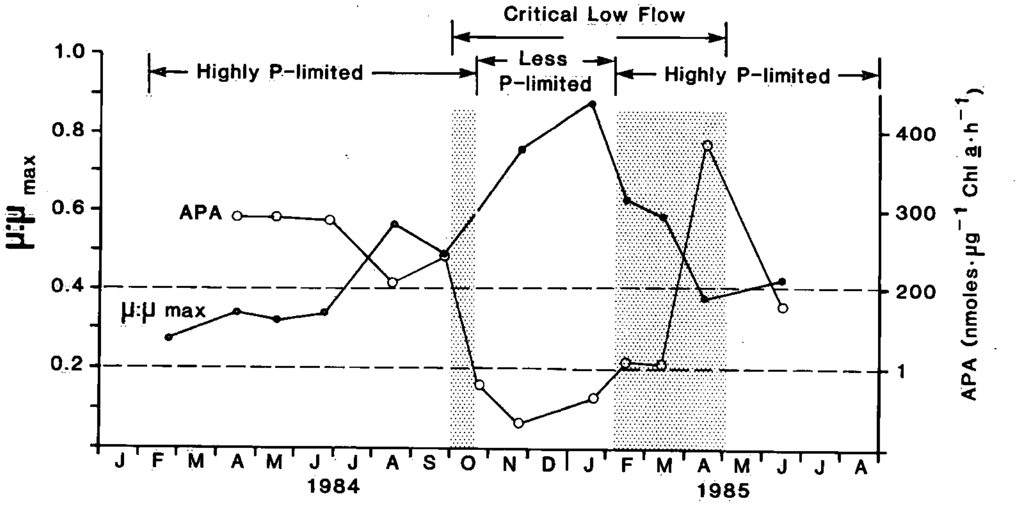

**Figure 7.** Seasonal changes in relative specific growth rates and alkaline phosphatase activity (APA) in the South Thompson River periphyton algae. The critical low flow period of the year and the times of high phosphorus deficiency are outlined. Shaded areas mark those times of the year when these two conditions overlap.

Another major factor affecting algal accumulation in rivers is water flow. Usually, algae in the Thompson River accumulate and become a problem only during periods of low, stable flow. Furthermore, at low flows the elevation in P-concentration from point source loadings is higher by virtue of lower dilution. The critical low flow period in the Thompson River is normally from October through April (Fig. 7). The time intervals when critical low flow coincides with periods of high phosphorus deficiency are indicated by the shaded areas in Figure 7. There are two periods each year when the river is most sensitive to phosphorus pollution: one, a short period in fall (October), and another longer period from February through April.

## Prediction of Algal Response to Phosphorus Control Measures

The amount of algae on rocks in the river is the main issue for environmental managers concerned with nutrients and eutrophication. For this reason and because of the discrepancy between the response of specific growth rate and sustainable biomass to P-addition, only the SB curves are used for predictive purposes.

Different SB curves were obtained at different times of the year (Fig. 5). Because the river is more sensitive to P-loading when it is more P-deficient, the SB data set from the period of high P-limitation has been used to predict the potential lowering of algal biomass in the river resulting from P-removal from the Weyerhaeuser Canada discharge. This should liberally estimate the influence of phosphorus loading on the river at other times of the year.

Prerequisite to estimating the effect of potential reductions of phosphorus loadings to the river is knowledge of what the present discharge is adding. Figure 9 shows the calculated dilution curve of the

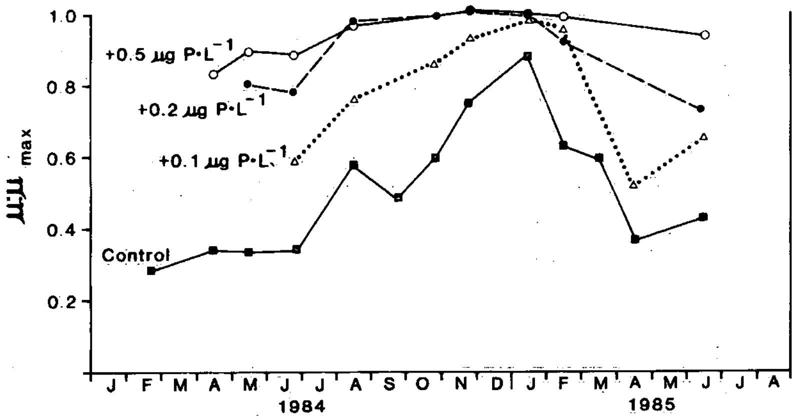

Figure 8. Relative specific growth rates of algae throughout the year at low levels of phosphate addition.

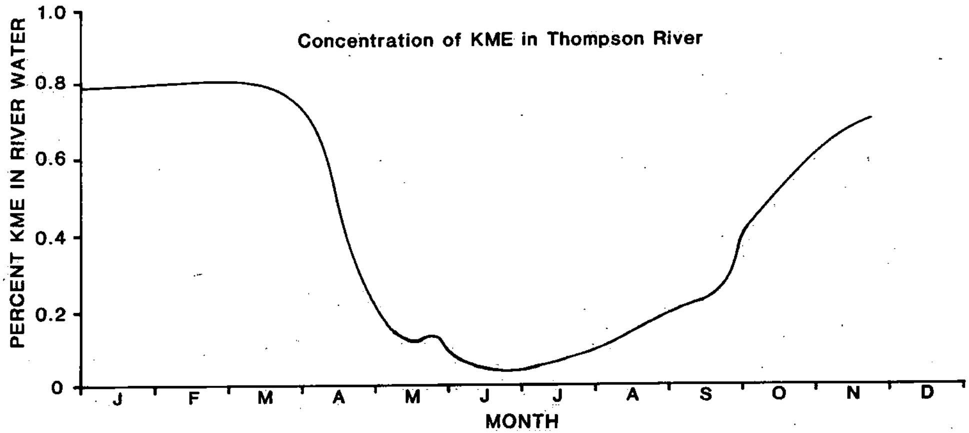

Figure 9. Dilution of the kraft mill effluent (KME) in the Thompson River assuming a steady effluent discharge rate of 1.68 $m^3 \cdot s^{-1}$, and streamflow data for the Thompson River at Spences Bridge.

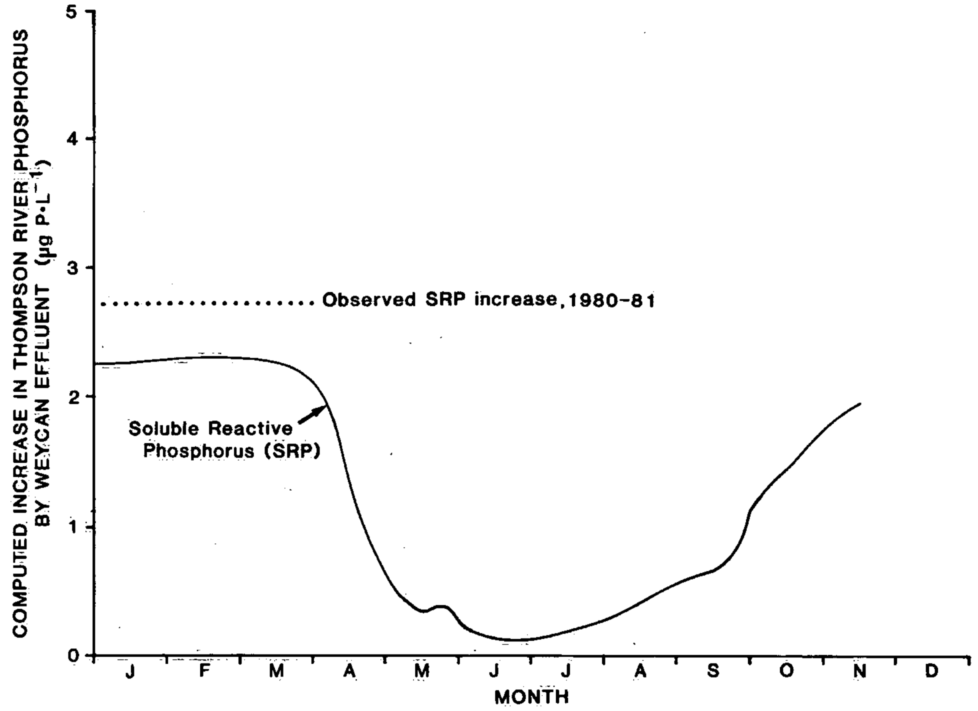

**Figure 10.** Downstream increases in soluble reactive phosphorus (SRP) due to the discharge of kraft mill effluent to the Thompson River. Computations assume the dilution curve in Figure 9 and an average SRP content of the effluent of 300 ppb.

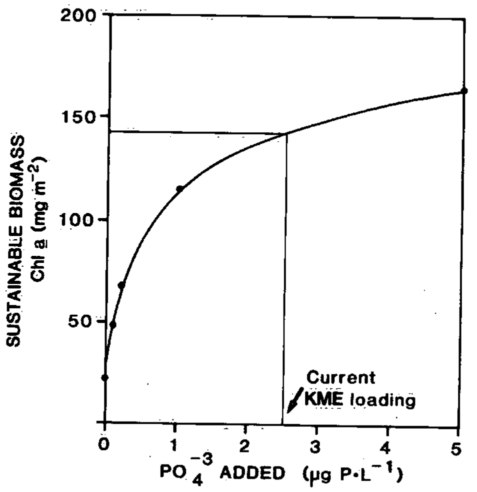

**Figure 11.** Sustainable algal biomass during high phosphorus limitation period (Feb.-Mar.) in response to phosphorus additions from the kraft mill effluent (KME). The algal biomass resulting from the current KME loading is shown.

kraft mill effluent (KME) in the Thompson River using an assumed constant effluent discharge of 1.68 m$^3$·s$^{-1}$ (J. Zagar, Weyerhaeuser Canada Ltd., pers. comm.) and mean monthly flow data for the Thompson River at Spences Bridge from Environment Canada data. Estimates of the concentrations of readily available dissolved phosphorus in the KME from both chemical measurements and radiobioassays are around 300 ppb (Jasper and Bothwell, 1986). Using values of 300 ppb for the SRP content of the KME and the dilution curve in Figure 9, the calculated increase in available soluble phosphorus concentration in the Thompson River is shown in Figure 10. The computed increases in SRP during low flow closely match the increases observed in the lower Thompson River during the winter of 1980–81 (Fig. 10; Bothwell, 1985). Keeping in mind the variation and measurement errors in all of these parameters, as well as the many simplifying assumptions made in this computation, the best estimate is that during annual low flow the present KME discharge elevates the SRP content of the Thompson River by approximately 2.5 ppb.

SB data from the long-term biomass accumulation experiment run during the period of higher P-limitation (Feb.-Mar. 1984) are plotted in Figure 11, with the data points connected by a smooth curve. Here it can be seen that at present

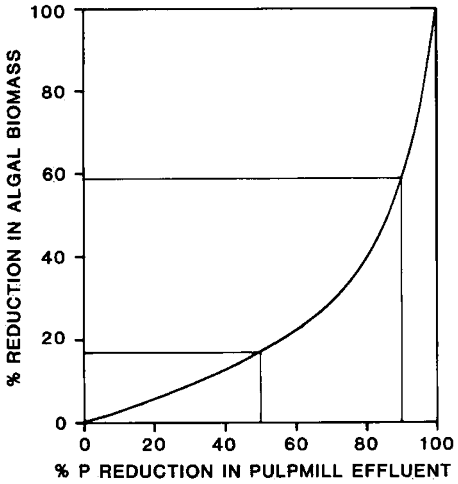

Figure 12. Curve showing, on a percentage basis, the expected decline in algal biomass as a function of the percentage reduction in soluble available phosphorus from the pulpmill effluent.

KME loading levels, the sustainable algal biomass is increased from 22.3 mg Chl $a \cdot m^{-2}$ to 142.4 mg Chl $a \cdot m^{-2}$. Taking these two values as the natural background level and the present elevated level of algae due to the current P-loading from the KME discharge, respectively, it is possible to calculate the relative improvement from known reductions in the loading. A graphic presentation of this computation is shown in Figure 12. A 50% reduction in the soluble-P output of the pulpmill would be expected to result in less than a 20% reduction in algal biomass downstream. To elicit a major reduction in downstream biomass, i.e. a 60% decrease in algae, would require a 90% reduction in the current P-loading of SRP from the KME.

There are many assumptions made in these computations, not the least of which is the validity of extrapolating from experimental troughs to a whole river ecosystem. Some of the conditions during experiments at EXTRA would tend to overestimate the influence of nutrients. Most important in this category is the low grazing pressure exerted on algal biomass in the troughs relative to what probably occurs in the river. Other key assumptions would underestimate the effect of phosphorus. The most important of these is the implicit acceptance that downstream declines in dissolved phosphorus are minimal (Bothwell and Daley, 1981). If significant declines do occur, the river will be more sensitive to P-loading than Figure 12 would indicate.

In spite of the above qualifications, the present attempt to predict the environmental consequences of an altered nutrient loading regime to a river is based on the best scientific data available. Wherever possible, environmentally conservative estimates have been used. For example, it was assumed that the background phosphorus levels at the point of mill discharge to the Thompson River are as low as those of the South Thompson River near Chase. However, the data from 1980–81 indicated that the background levels of the North Thompson are higher than those of the South Thompson, so the combination of the two rivers must have higher levels than the southern tributary alone.

Another important factor relevant to making decisions about future nutrient control measures on the Thompson River is the general observation that in recent years the massive algal accumulations common in the 1970's are no longer occurring. While there is no readily apparent explanation for this, it is possible that the invertebrate communities in the river have adapted to the new higher levels of production and are now better able to keep algal biomass under control. More detailed studies on the invertebrate communities in the river might provide an answer to this important question.

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# Glossary

alkaline phosphatase activity (APA): An enzyme produced by many microbial cells in response to phosphorus deficiency. A high level means the cells are P-deficient and a low level means they are P-replete.

chlorophyll (Chl *a*): A plant pigment used to quantify the amount of algae.

maximum specific growth rate ($\mu_{max}$): The maximum division rate for cells under the restraints imposed by the physical environment, e.g., temperature and light. At this growth rate, the cells are not limited by any nutrient and are growing as fast as biologically possible.

maximum sustainable biomass ($SB_{max}$): The highest sustainable biomass value as a function of enrichment observed in each experiment was termed the maximum sustainable biomass and was used to normalize the other values.

orthophosphate: The molecular form of phosphorus that is most readily used by microorganisms.

relative specific growth rate ($\mu$:$\mu_{max}$): An index of how nutrient deficient the cells are. Their specific growth rate ($\mu$) divided by the maximum specific growth rate ($\mu_{max}$) under the existing physical conditions.

soluble reactive phosphorus (SRP): Those forms of dissolved phosphorus in water that are measured by standard chemical techniques not using digestion. Most of this is presumed to be orthophosphate.

specific growth rate ($\mu$): The number of divisions per day of a microbial cell. This is a measure of how fast the cells are growing and is independent of how many there are.

sustainable biomass (SB): The highest chlorophyll values at the end of each experiment were averaged and used as a measure of the maximum amount of algae that could exist per unit surface area under the experimental conditions.

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